Institute Neuroscience de la Timone

14.02.2020

Effects of attention on visual processing between cortical layers and cortical areas V1 and V4

Invited speaker:

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Center for Mind/Brain Sciences, CIMeC, University of Trento,
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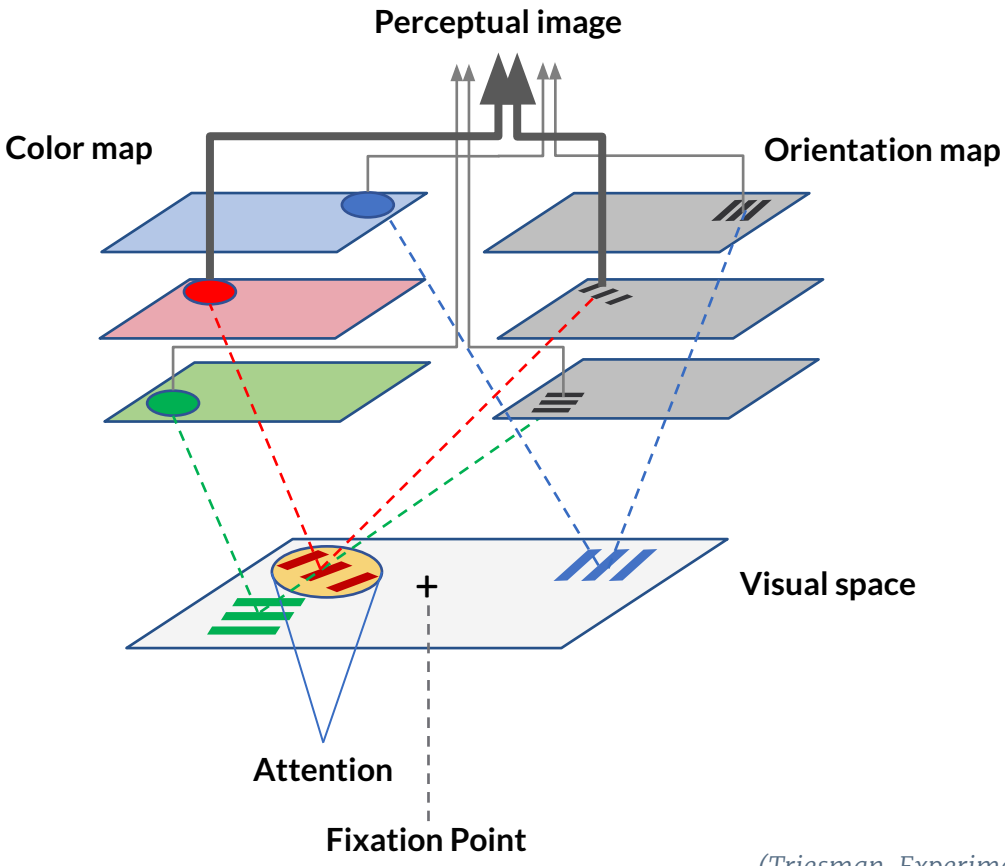
Visual Attention / Introduction

- **Attention improves sensory processing, perceptual readout and behavior.**

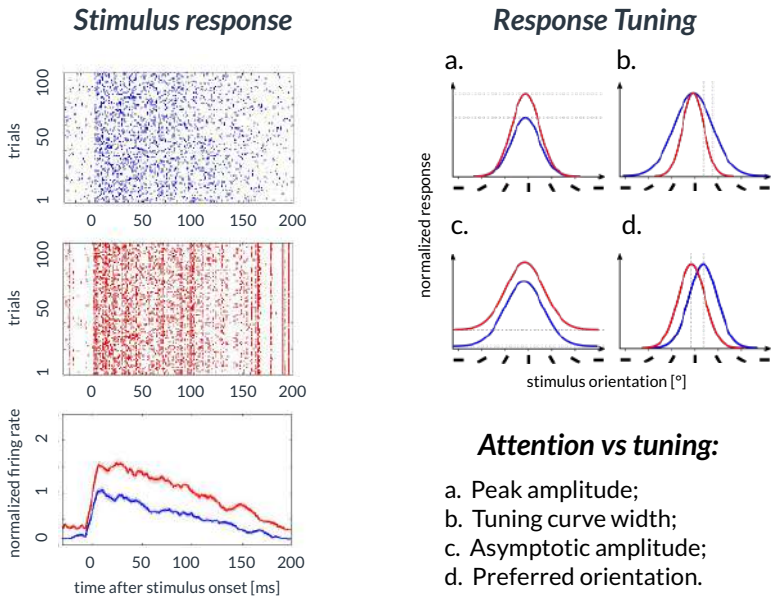


(Triesman, Experimental psychology society 1988)

Visual Attention / Introduction

- **Attention improves sensory processing, perceptual readout and behavior.**
- **How does attention affect neural signals?**

Spiking activity

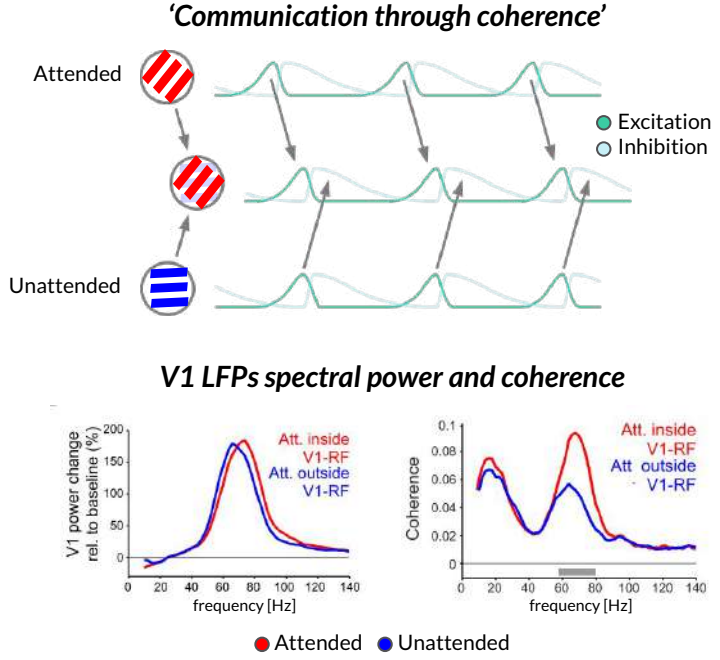


Attention vs tuning:

a. Peak amplitude;
b. Tuning curve width;
c. Asymptotic amplitude;
d. Preferred orientation.

(Moran & Desimone, 1985; Treue & Maunsell 1996; McAdams & Maunsell, 1999; Cohen & Maunsell 2009; Thiele et al., 2016; […])

Local Field Potentials (LFPs)

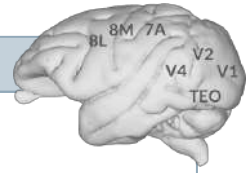


(Fries, 2005; Bosman et al., 2012; Fries, 2015; […])

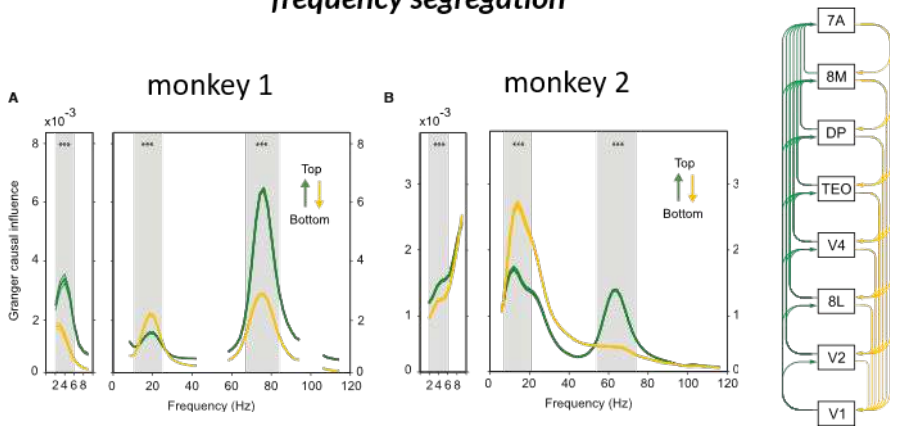
Visual Attention / Introduction

- **Attention improves sensory processing, perceptual readout and behavior.**
- **How does attention affect neural signals?**
- **How do visual cortical structures interact?**

Interactions *between* cortical areas



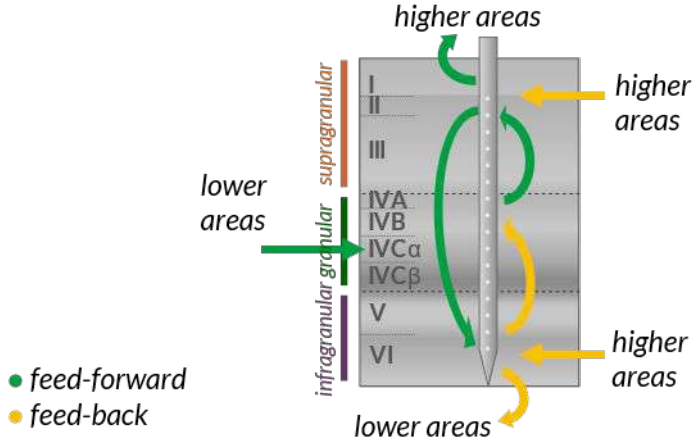
'feed-forward vs feed-back frequency segregation'



(Felleman & van Essen, 1991; Bastos et al., 2015; van Kerkoerle et al., 2014; [...])

Interactions *within* cortical areas

'Canonical neocortex circuit model'

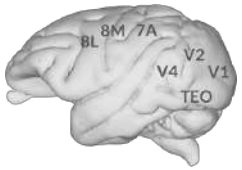


(Douglas & Martin, 1991; Shipp, 2007; Bastos et al., 2012; Markov et al., 2014; [...])

Visual Attention / Introduction

- **Attention improves sensory processing, perceptual readout and behavior.**
- **How does attention affect neural signals?**
- **How do visual cortical structures interact?**

STUDY AIMS:



***between** areas*

***within** areas*

Combine

Visual attention

→ *Analysis of laminar signals from **2 macaque monkeys** performing **visual spatial attention task**;*

→ *Signals recorded **simultaneously in V1 and V4** at **multiple laminar depths**;*

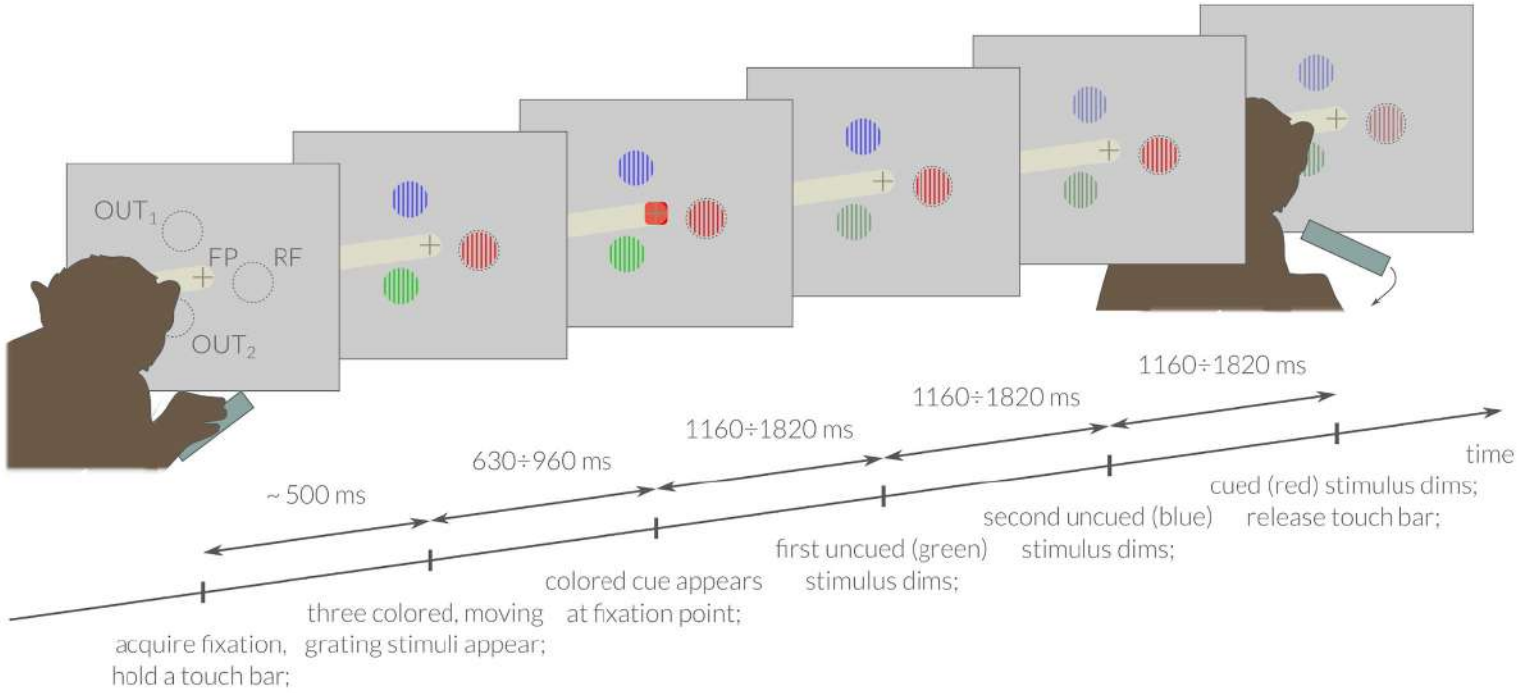
→ *Spectral features: **spectral power** and **spectral coherence** of LFP signals;*

→ *Directionality: **Granger-causal** influences **within V1**, **within V4**, and **between V1 and V4**.*

Outline

- ***Preliminary stages***
- *Spectral power and attention*
- *Spectral coherence and attention*
- *Granger-causality and attention*
- *Results summary*
- *Conclusions*

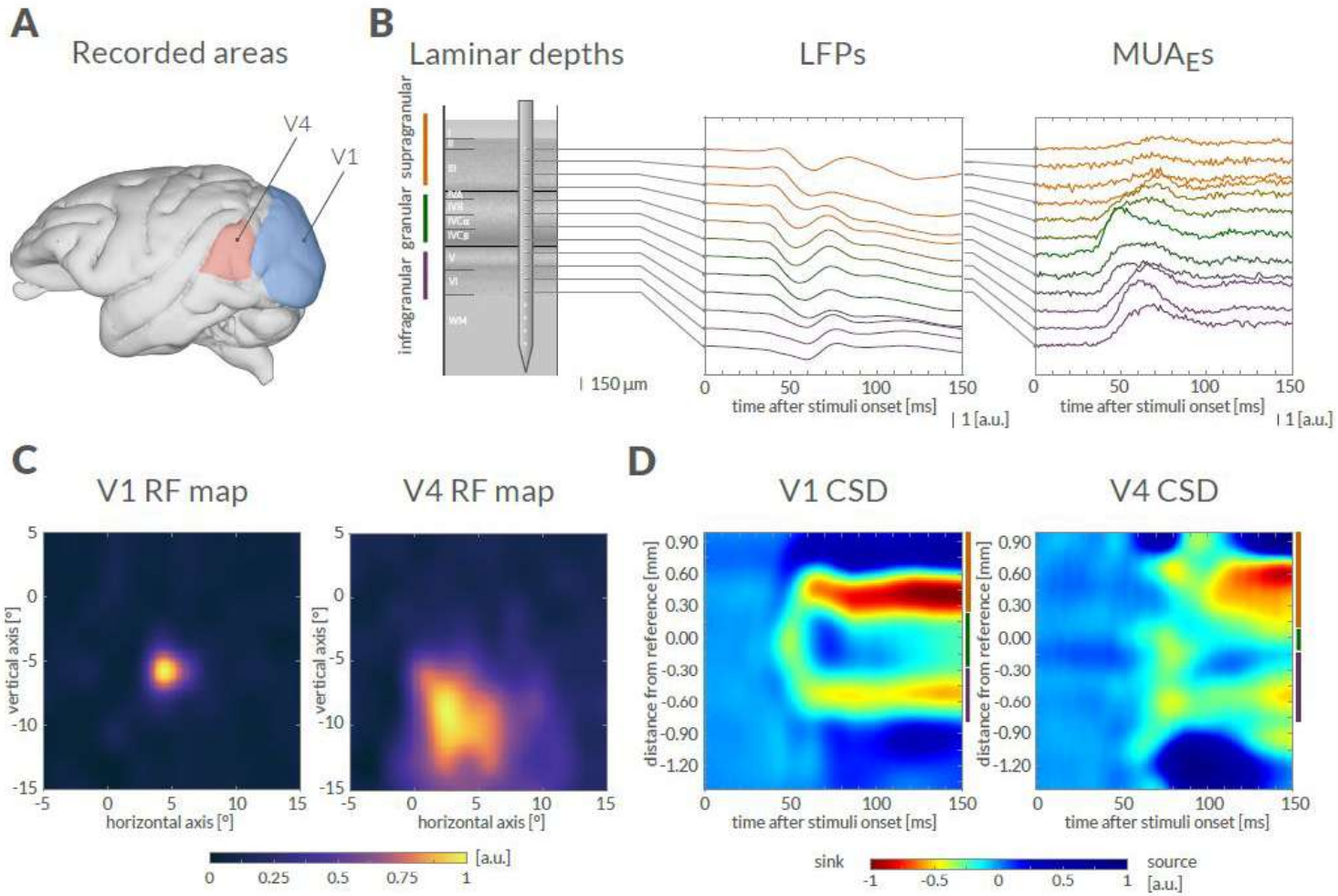
Visual Attention / Behavioral task



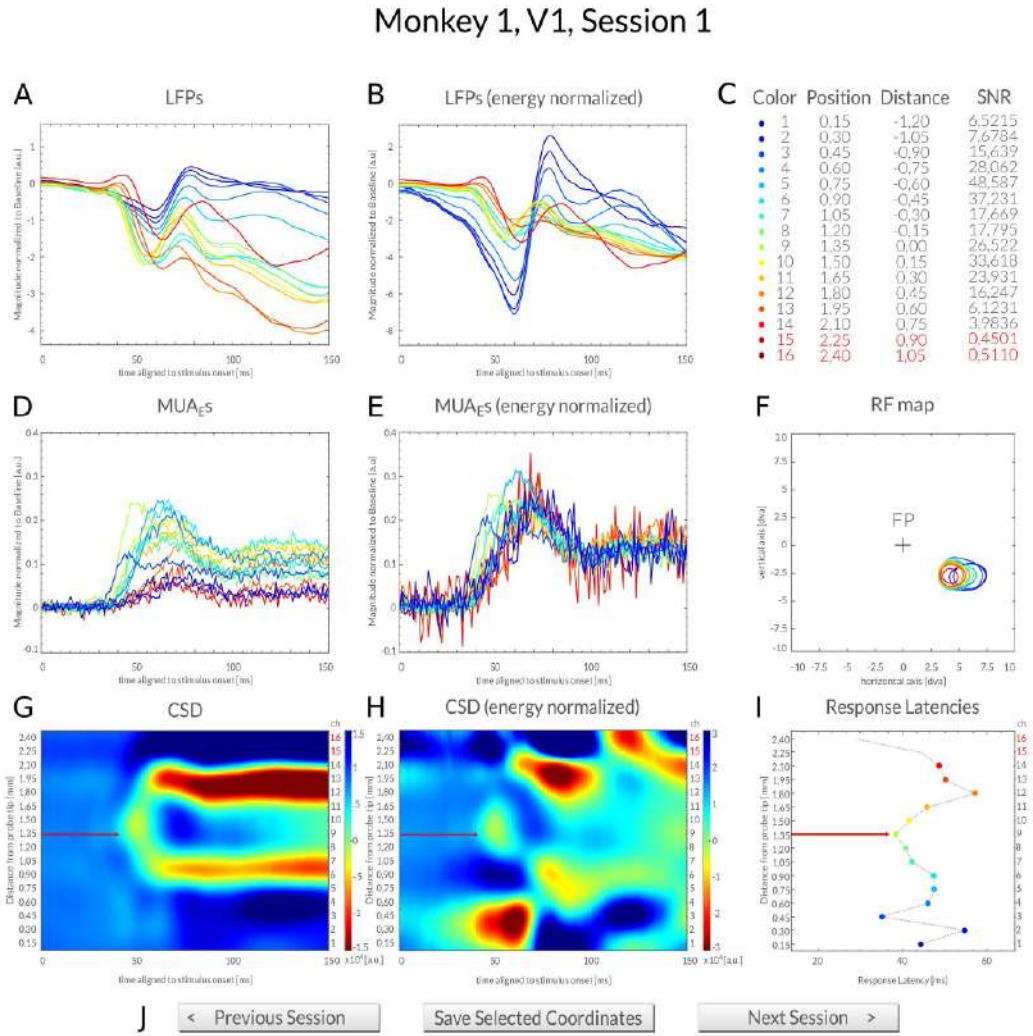
Newcastle University
Institute of Neuroscience

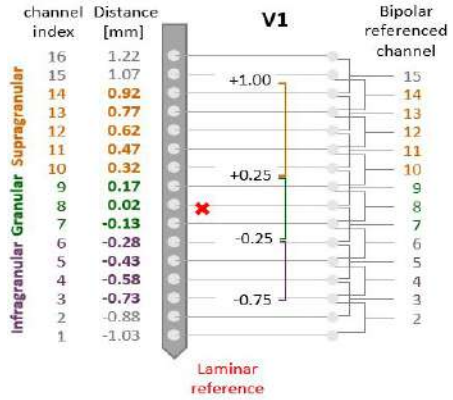
- *Two monkeys (macaca mulatta) respectively aged 9 and 11 years by the time of recordings.*
- *Experiments performed at Newcastle University, Institute of Neuroscience by: Michael Boyd, PhD, Jochem vam Kempen, PhD candidate, under the supervision of Prof. Alexander Thiele.*

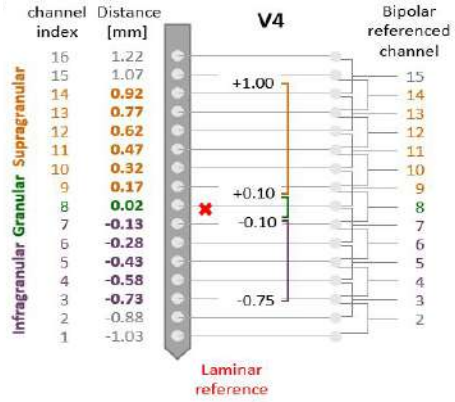
Preliminary stages / Recording setup



Preliminary stages / Laminar alignment







Outline

- ***Preliminary stages***
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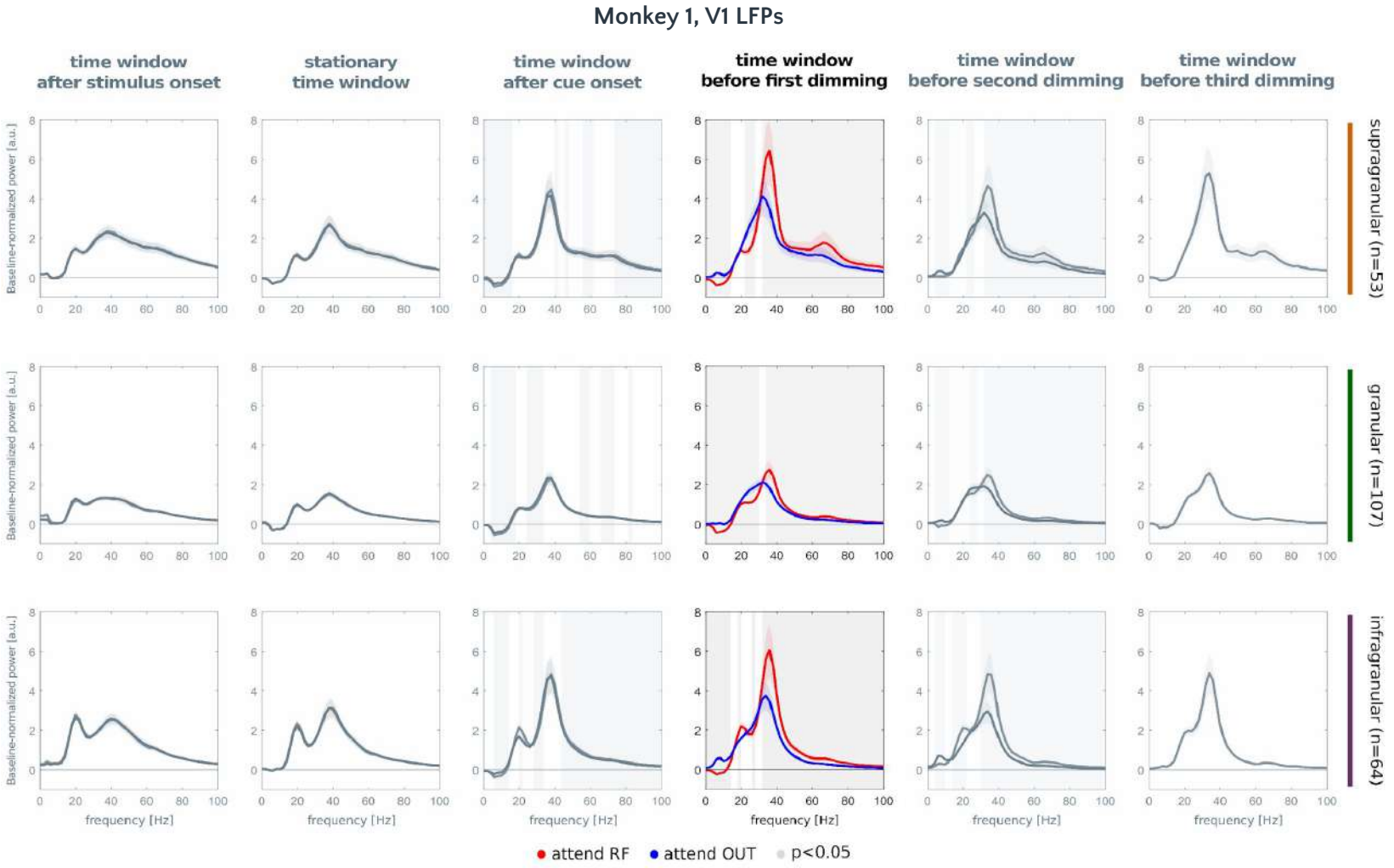
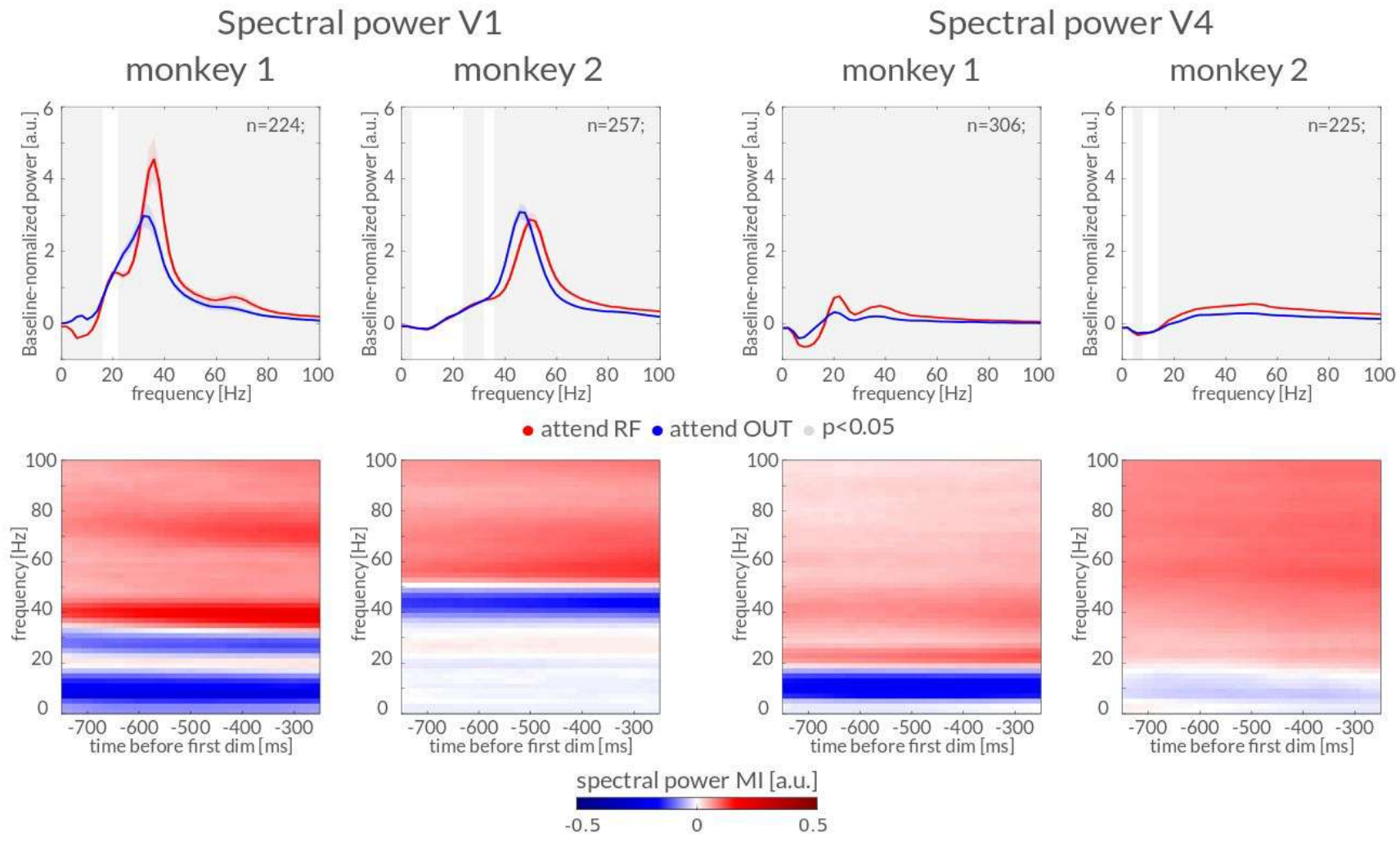
Visual Attention / Spectral Power



Spectral Power

- *Average +/- s.e.m. across sessions*
- *Pooled by laminar compartments*
- *Multi-trial estimation (pooled across trials)*
- *Multi-taper estimation normalized to pre-stimulus mean power. K=3 tapers, TW=2.*

Visual Attention / Spectral Power



Spectral Power

- *Average +/- s.e.m. across sessions and laminar depths*
- *Multi-trial estimation (pooled across trials)*
- *Multi-taper estimation normalized to pre-stimulus mean power. K=3 tapers, TW=2.*

Spectral Power Modulation Index

$$\frac{P(att.RF) - P(att.OUT)}{P(att.RF) + P(att.OUT)}$$

Multi-taper estimation normalized to pre-stimulus mean power. K=3 tapers, TW=2.

Visual Attention / Mutual Information

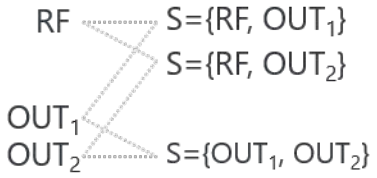
Information between:

- Attended stimulus (color, location) ***S;***
- Laminar LFP Response ***R.***

$$\boldsymbol{I(S;R)} = \sum_{\substack{s\in S \\ r\in R}} p(s,r)\log_2\left(\frac{p(s,r)}{p(s)p(r)}\right)$$

Attended stimulus *S:*

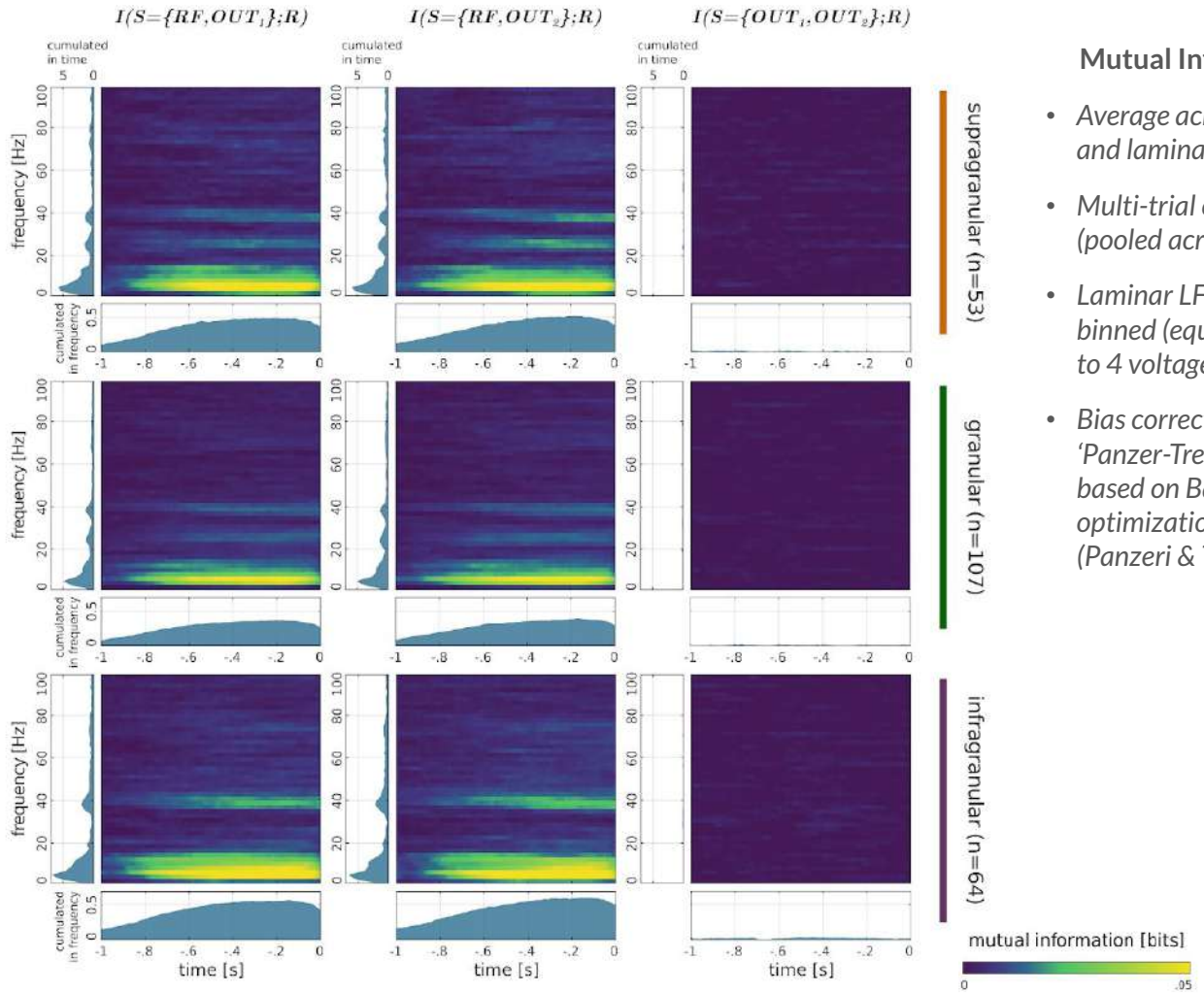
Trials were collected in groups.



Laminar LFP Response *R:*

Instantaneous Hilbert amplitude of LFP signals frequency-demodulated by narrow-band filtering every 2Hz;

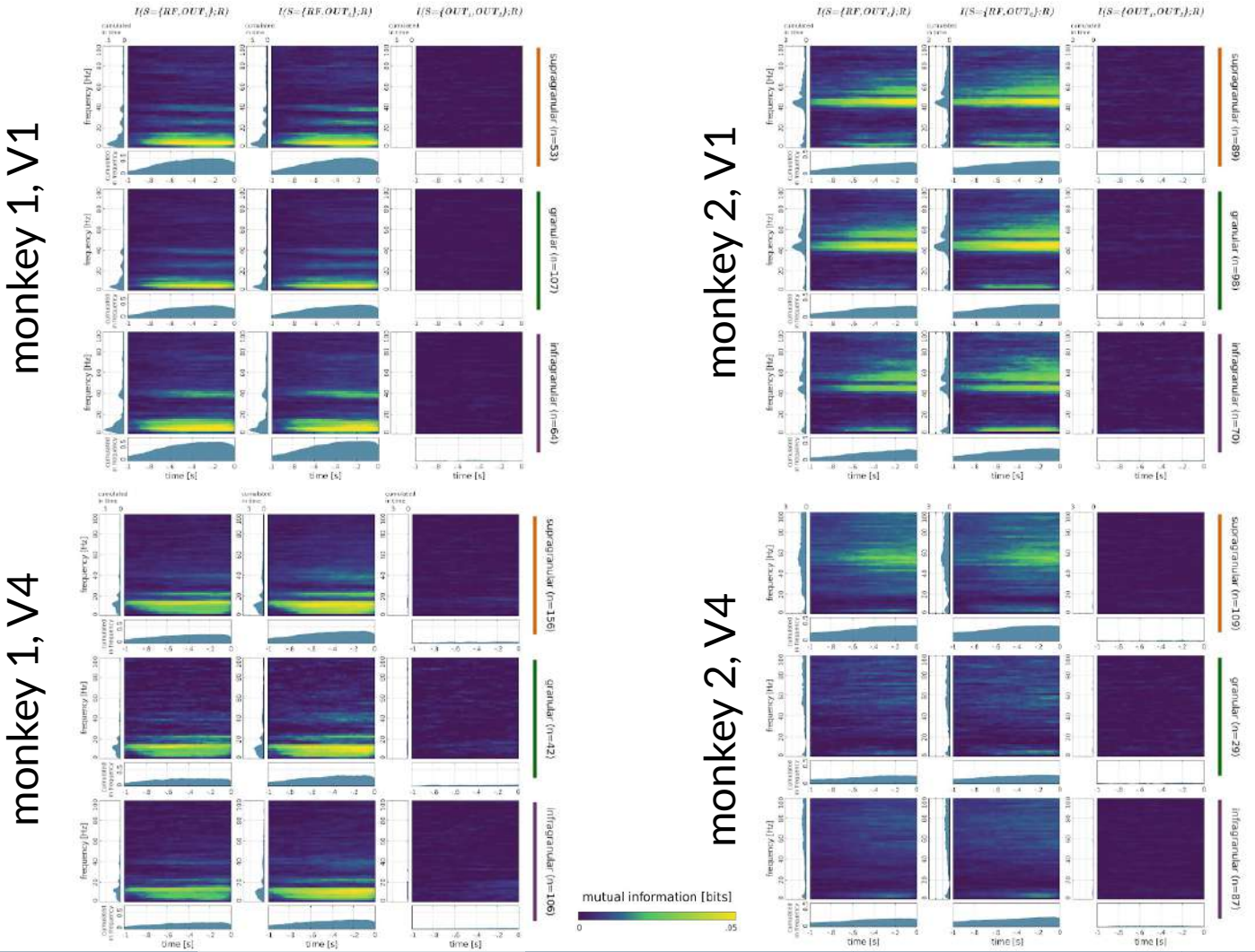
monkey 1, V1



Mutual Information

- *Average across sessions and laminar depths*
- *Multi-trial estimation (pooled across trials)*
- *Laminar LFP responses binned (equi-populated) to 4 voltage level bins.*
- *Bias correction: 'Panzer-Treves' method, based on Bayesian optimization (Panzeri & Treves, 1996)*

Visual Attention / Mutual Information



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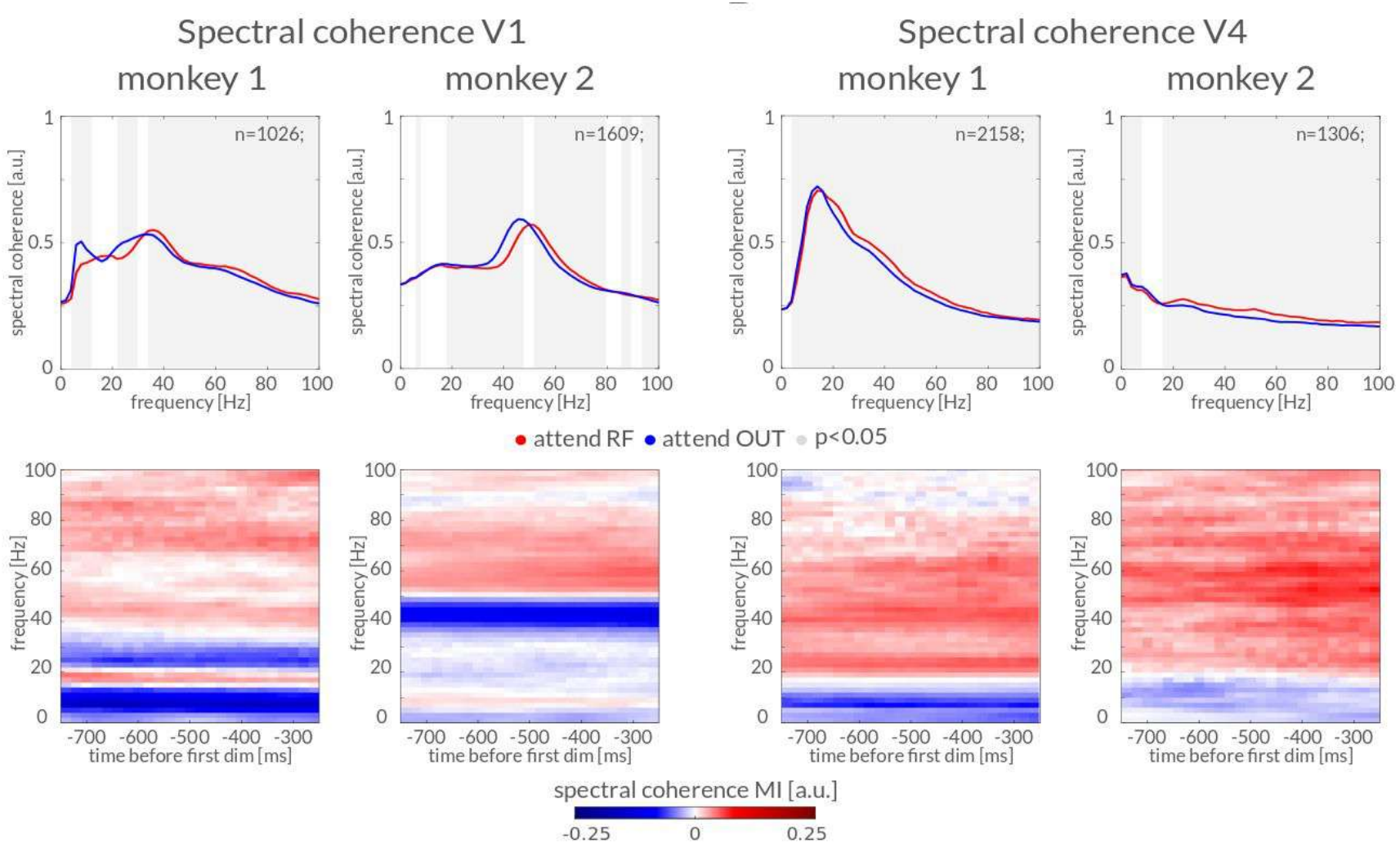
Visual Attention / Spectral coherence



Spectral Coherence

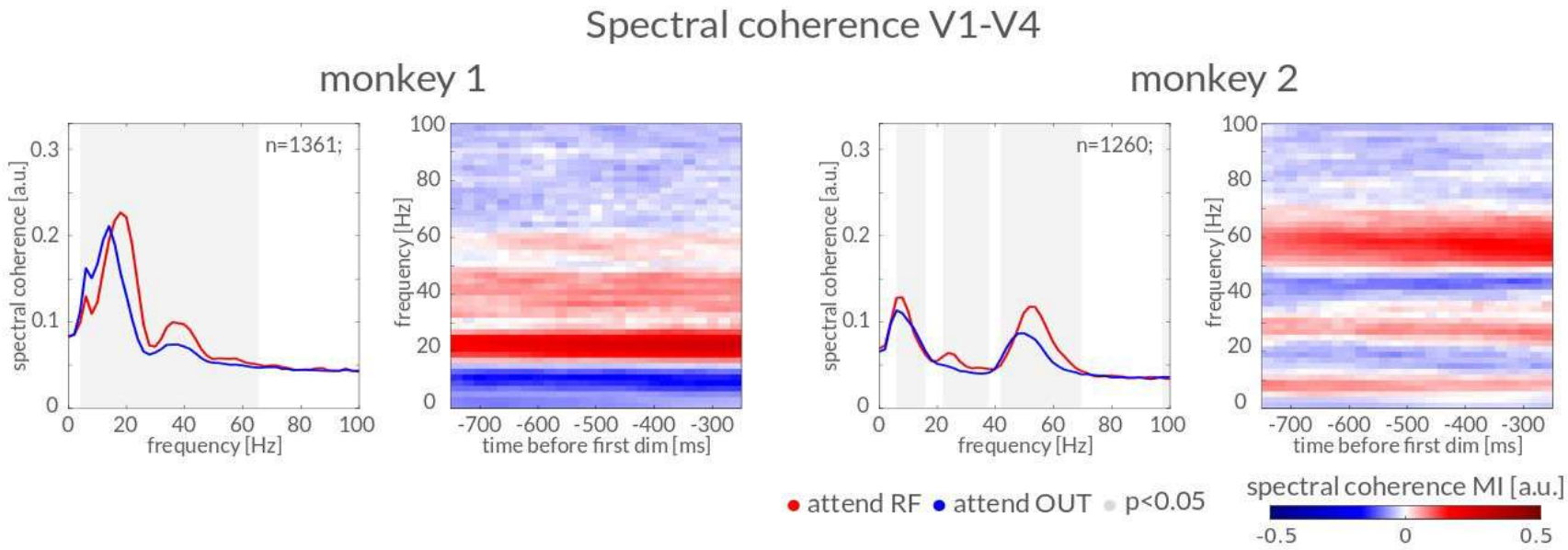
- *Average +/- s.e.m. across sessions and laminar depth pairs*
- *Multi-trial estimation (pooled across trials)*
- *Multi-taper estimation K=3 tapers, TW=2.*

Spectral Coherence Modulation Index

$$\frac{S(att.RF) - S(att.OUT)}{S(att.RF) + S(att.OUT)}$$

Multi-taper estimation K=3 tapers, TW=2.

Visual Attention / Spectral coherence



Spectral Coherence Modulation Index

$$\frac{S(att.RF) - S(att.OUT)}{S(att.RF) + S(att.OUT)}$$

Average across sessions and laminar depth pairs

Multi-taper estimation K=3 tapers, TW=2.

Outline

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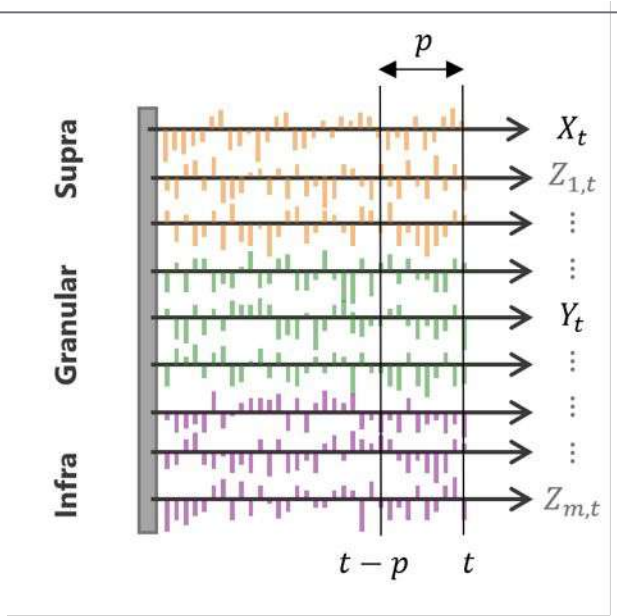
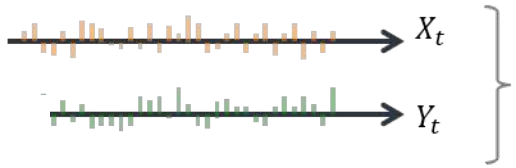
Granger causality / methods





Granger causality (GC)

$$GC_{Y\to X}$$

***i*) Vector Auto-Regressive (VAR(*p*)) Model**

$$\begin{pmatrix} X_t \\ Y_t \end{pmatrix} = \sum_{k=0}^{p} \begin{pmatrix} A_{xx,k} & A_{xy,k} \\ A_{yx,k} & A_{yy,k} \end{pmatrix} \begin{pmatrix} X_{t-k} \\ Y_{t-k} \end{pmatrix} + \begin{pmatrix} \varepsilon_{x,t} \\ \varepsilon_{y,t} \end{pmatrix} \qquad \mathbf{\Sigma} = \mathbf{cov} \begin{pmatrix} \varepsilon_{x,t} \\ \varepsilon_{y,t} \end{pmatrix}$$

***ii*) Reduced VAR(*p*) Model**

$$X_t = \sum_{k=0}^{p} A^{(r)}_{xx,k} X_{t-k} + \varepsilon^{(r)}_{x,t} \qquad \mathbf{\Sigma^{(r)}} = \mathbf{cov}\left(\varepsilon^{(\mathbf{r})}_{x,t}\right)$$

***iii*) Estimate GC**

$$\mathcal{F}_{Y\to X} = \ln\left(\frac{|\mathbf{\Sigma}^{(r)}_{xx}|}{|\mathbf{\Sigma}_{xx}|}\right)$$

$$f_{Y\to X}(\lambda) = \ln\left(\frac{|S_{xx}(\lambda)|}{|S_{xx}(\lambda) - H_{xy}(\lambda)(\mathbf{\Sigma}_{yy} - \mathbf{\Sigma}_{yx}\mathbf{\Sigma}^{-1}_{xx}\mathbf{\Sigma}_{xy}) H^{*}_{xy}(\lambda)|}\right), \qquad 0 \le \lambda \le F_s$$

VAR(p) transfer function

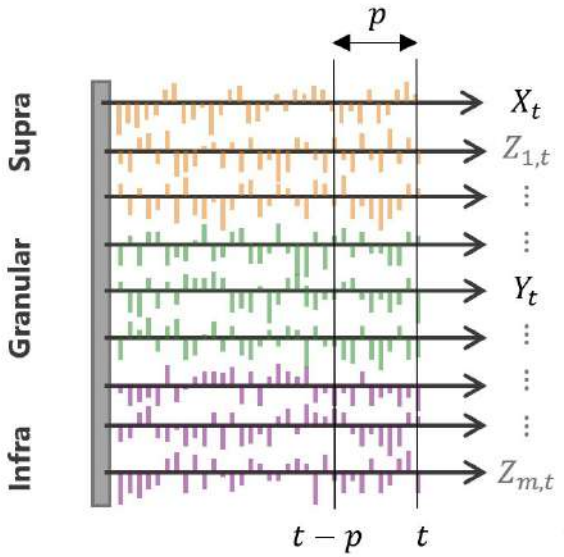
$$\mathbf{H}(\lambda) = (\mathbf{I} - \mathrm{fft}(\mathbf{A}_k, \lambda))^{-1}$$

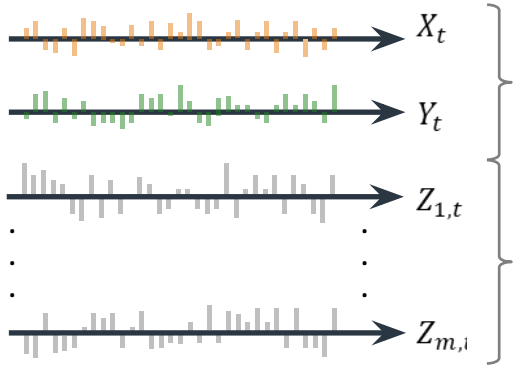
Cross-Power Spectral Density

$$\mathbf{S}(\lambda) = \mathbf{H}(\lambda) \cdot \mathbf{\Sigma} \cdot \mathbf{H}^{*}(\lambda)$$

(Granger, 1963; Geweke, 1982; Barnett & Seth 2014)

Granger causality / methods





Conditional GC (cGC)

$$cGC_{Y\to X|Z}$$

Estimate GC (in frequency)

$$f_{Y\to X|\mathbf{Z}}(\lambda) = f_{(Y;\mathbf{Z}')\to X'}(\lambda), \qquad 0 \le \lambda \le F_s/2$$

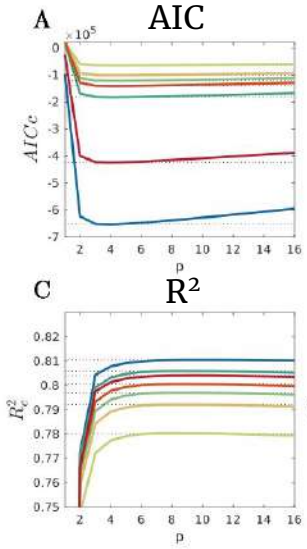
Vector Auto-Regressive (VAR(*p*)) Model

$$\begin{pmatrix} X'_t \\ Y_t \\ Z'_{1,t} \\ \vdots \\ Z'_{m,t} \end{pmatrix} = \sum_{k=0}^{p} \mathbf{A}'_k \begin{pmatrix} X'_t \\ Y_t \\ Z'_{1,t} \\ \vdots \\ Z'_{m,t} \end{pmatrix} + \begin{pmatrix} \varepsilon'_{x,t} \\ \varepsilon_{y,t} \\ \varepsilon'_{z_1,t} \\ \vdots \\ \varepsilon'_{z_m,t} \end{pmatrix}$$

(Granger, 1963; Geweke, 1982; Barnett & Seth 2014)

Granger causality / methods

Choice of *p* (VAR order) → *p*=10 time bins (~50 ms)



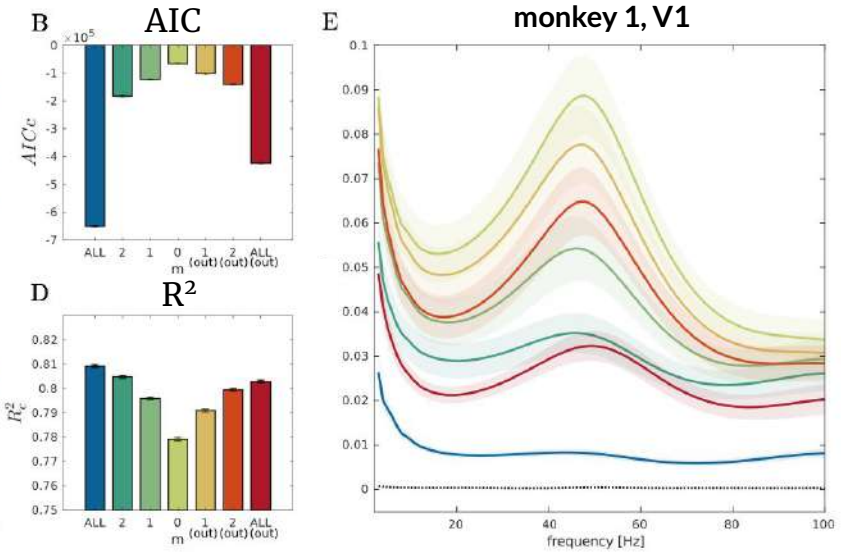
$$\rightarrow AIC = 2p(m+2)^2 - 2\log L$$
$$= 2p(m+2)^2 + M \log|\boldsymbol{\Sigma}|\ ;$$

$$\rightarrow R^2 = 1 - |\Sigma|^2 / |\boldsymbol{U}|^2.$$

$$(M = N_{tr}(N_{tp} - p))$$
$$(\boldsymbol{U} = (X\ Y\ \boldsymbol{Z}))$$

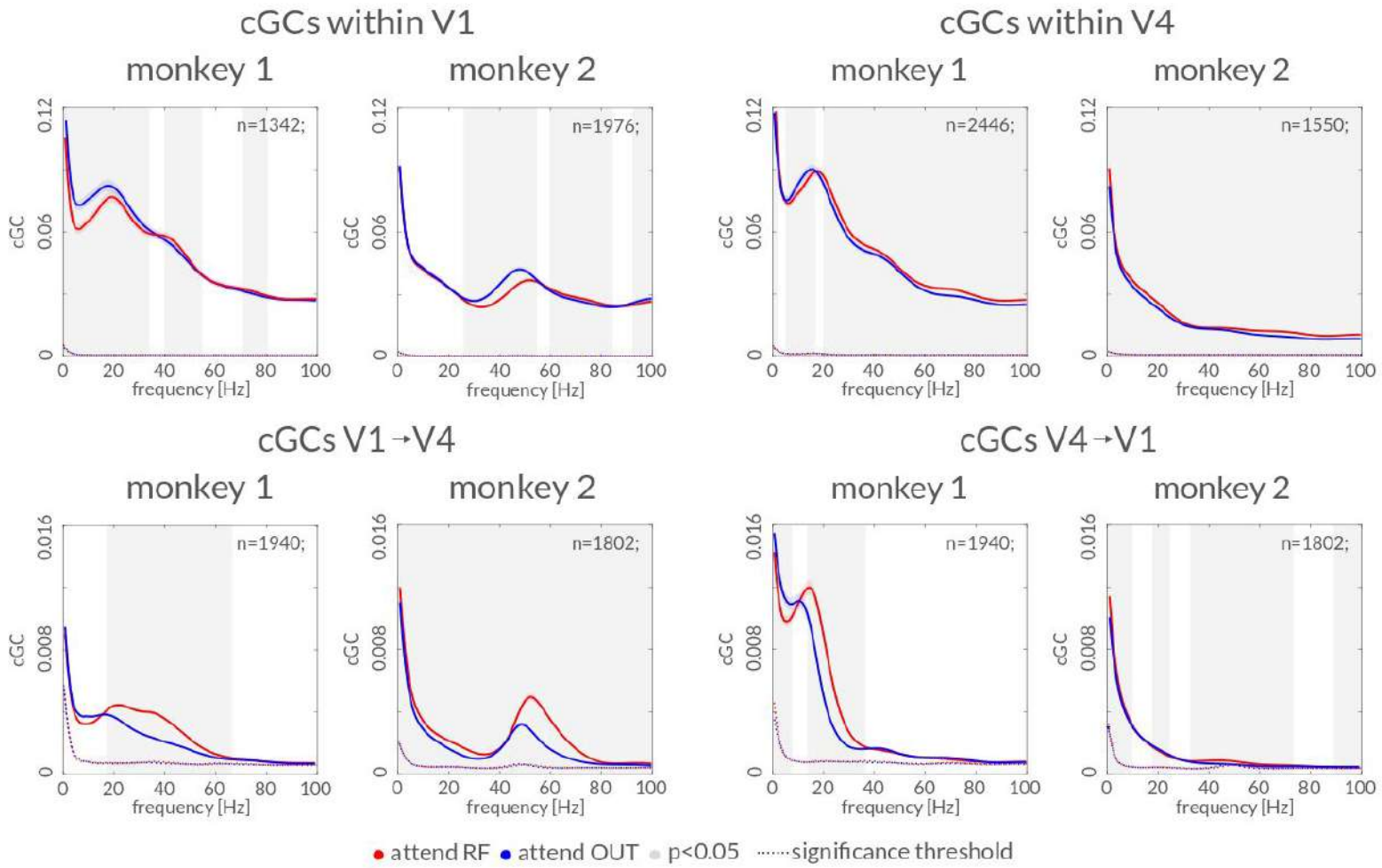
(Chen at al, 2006; Barnett and Seth, 2014)

Choice of *m* (conditioning variable) → *m=2(out)*



- ***m=ALL*** *(fully conditional);*
- ***m=2*** *most informative channels;*
- ***m=1*** *most informative channel;*
- ***m=0*** *(unconditional GC);*
- ***m=1 (out)*** *most inf. ch. outside the compartments of (X,Y) ;*
- ***m=2 (out)*** *most inf. ch.s outside the compartments of (X,Y);*
- ***m=ALL (out)*** *ch.s outside the compartments of (X,Y);*

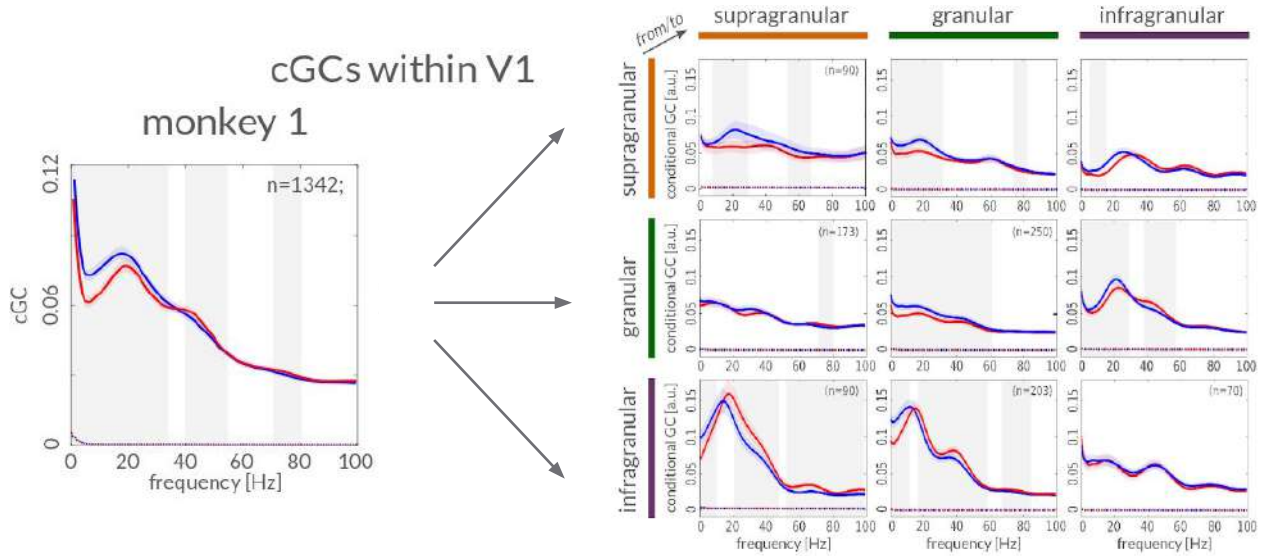
Visual Attention / Granger Causality



Granger causality

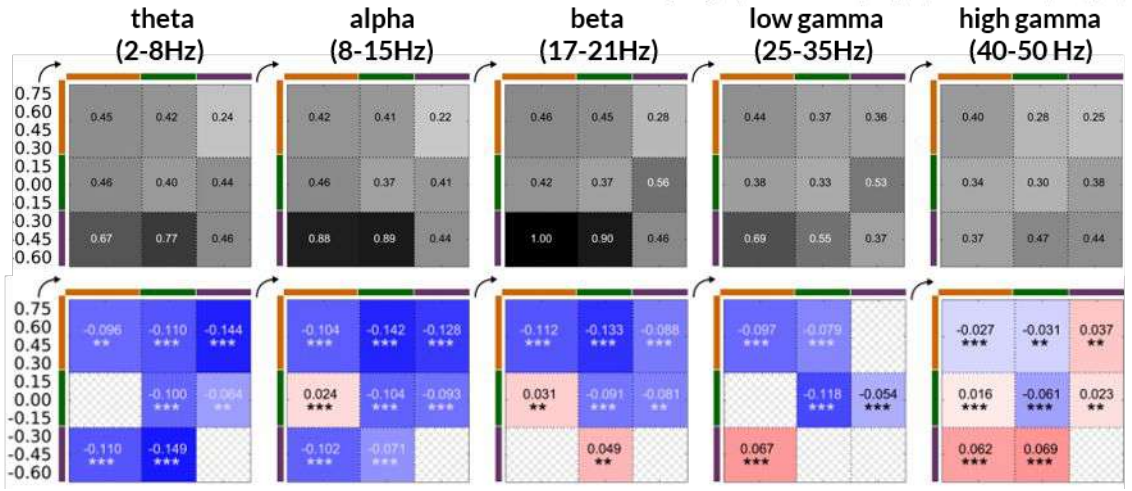
- *Average +/- s.e.m. across sessions and laminar depth directions*
- *Multi-trial estimation (pooled across trials, Barnett & Seth, 2014)*

Visual Attention / Granger Causality



GC Magnitude

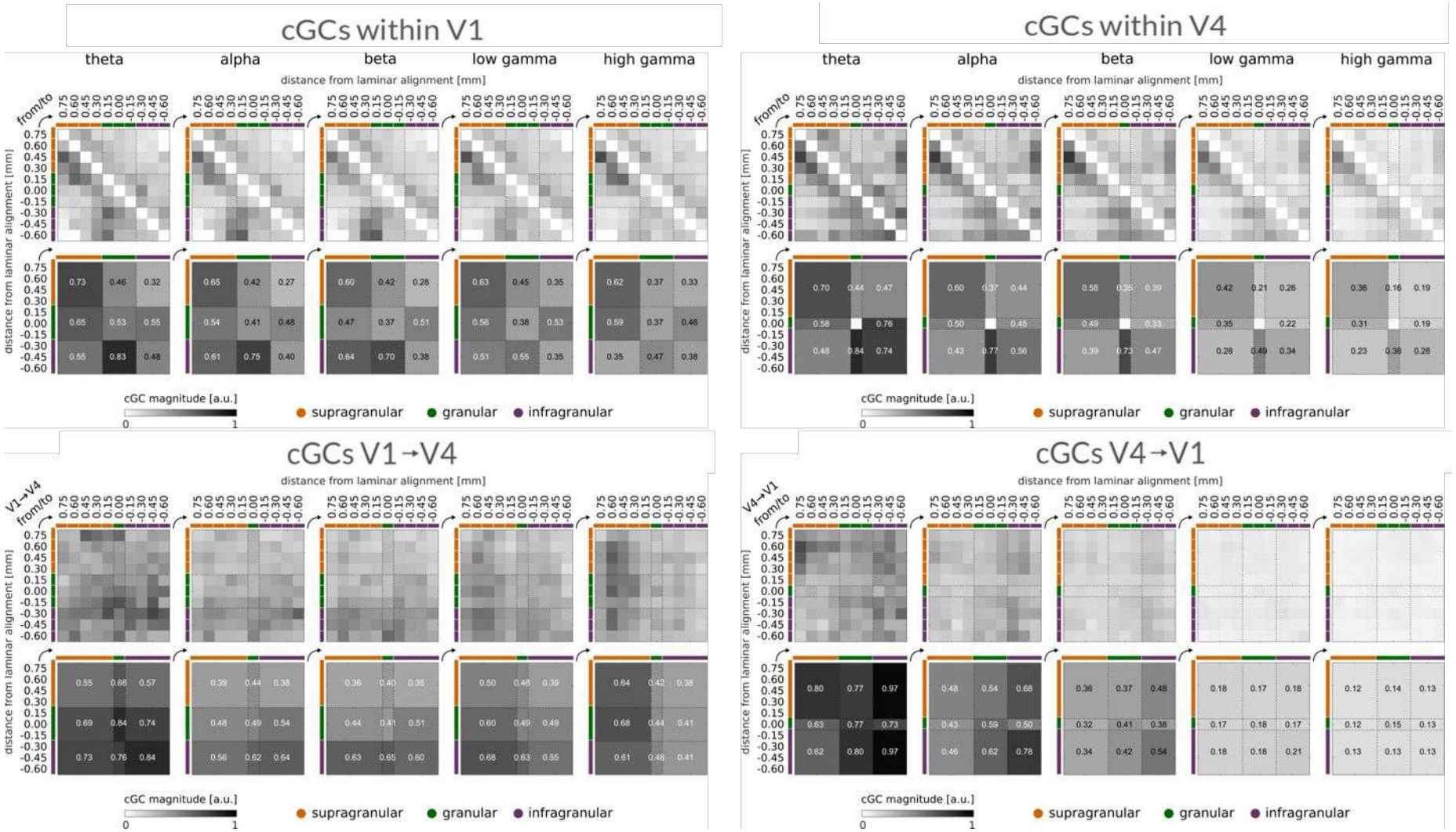
$$cGC = (cGC_{RF} + cGC_{OUT})/2$$



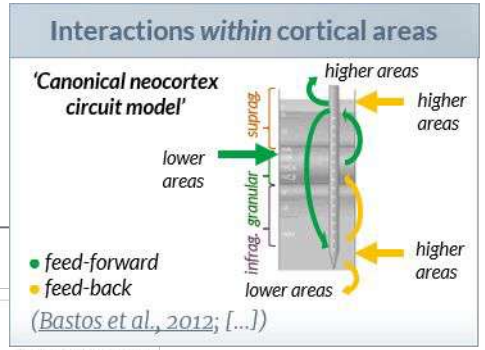
GC Modulation Index

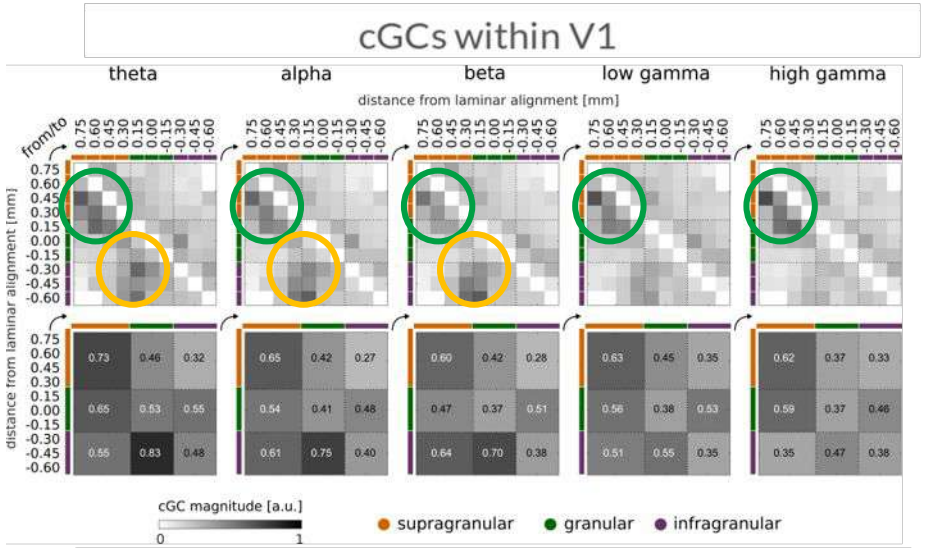
$$cGC_{MI} = \frac{cGC_{RF} - cGC_{OUT}}{cGC_{RF} + cGC_{OUT}}$$

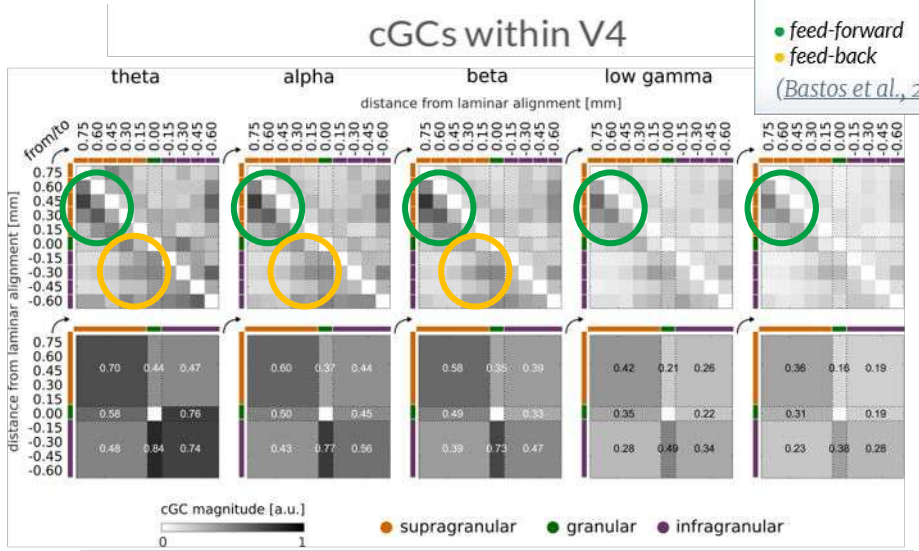
Visual Attention / Granger Causality

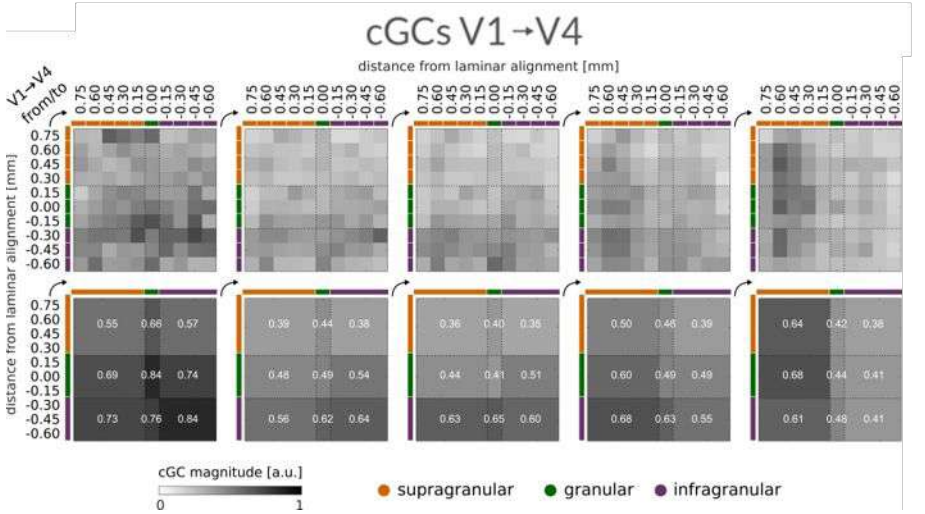


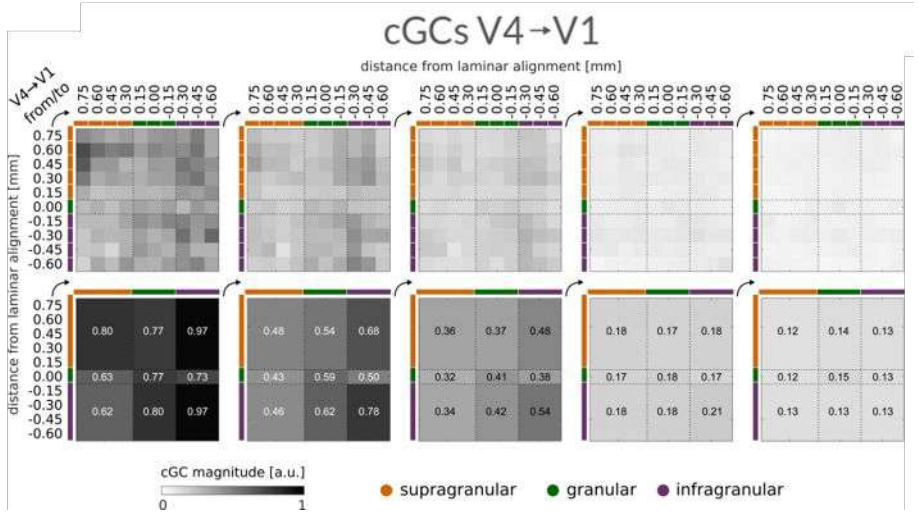
Visual Attention / Granger Causality



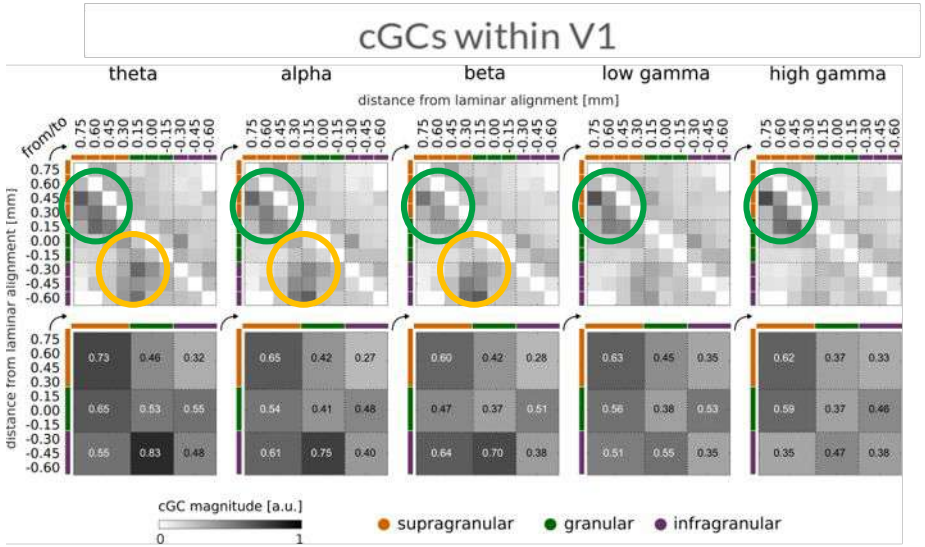


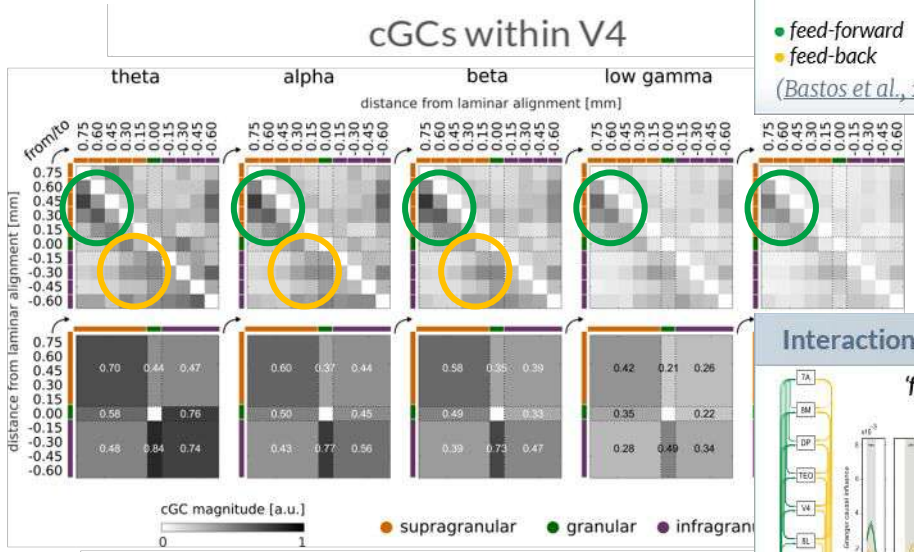


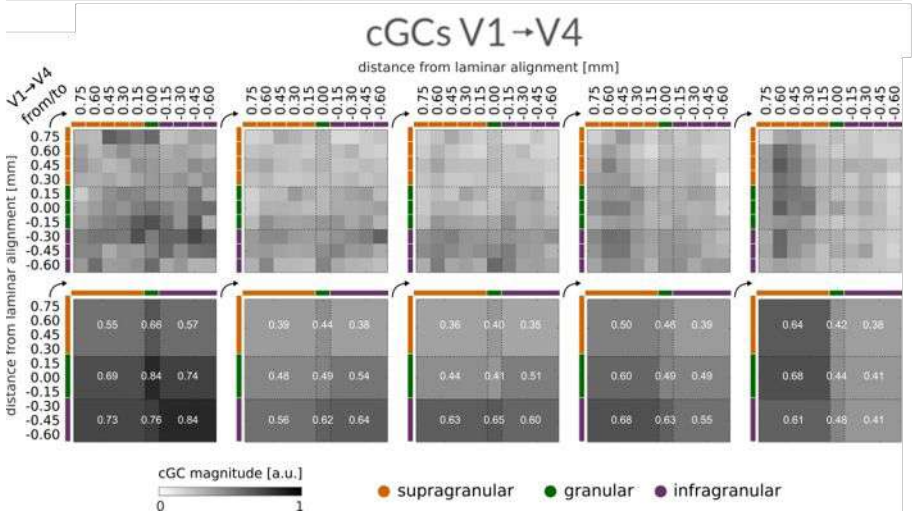


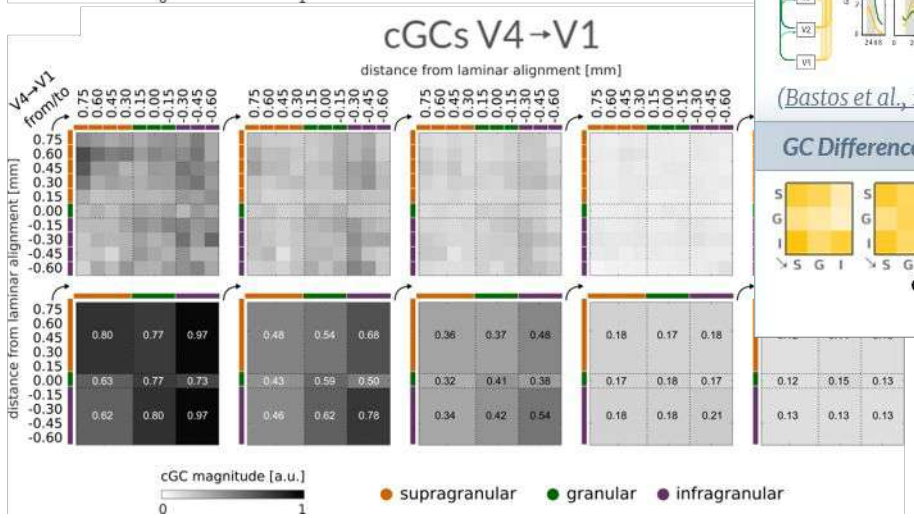


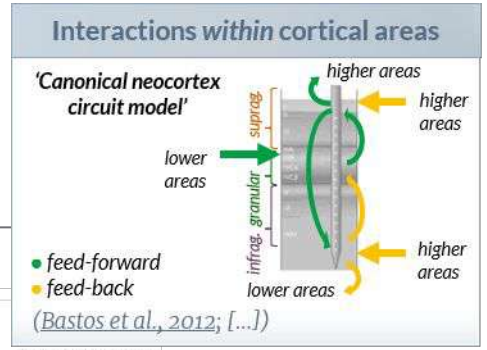
Visual Attention / Granger Causality

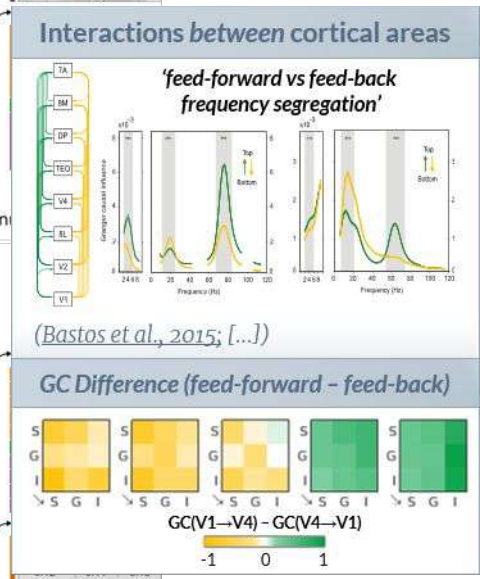




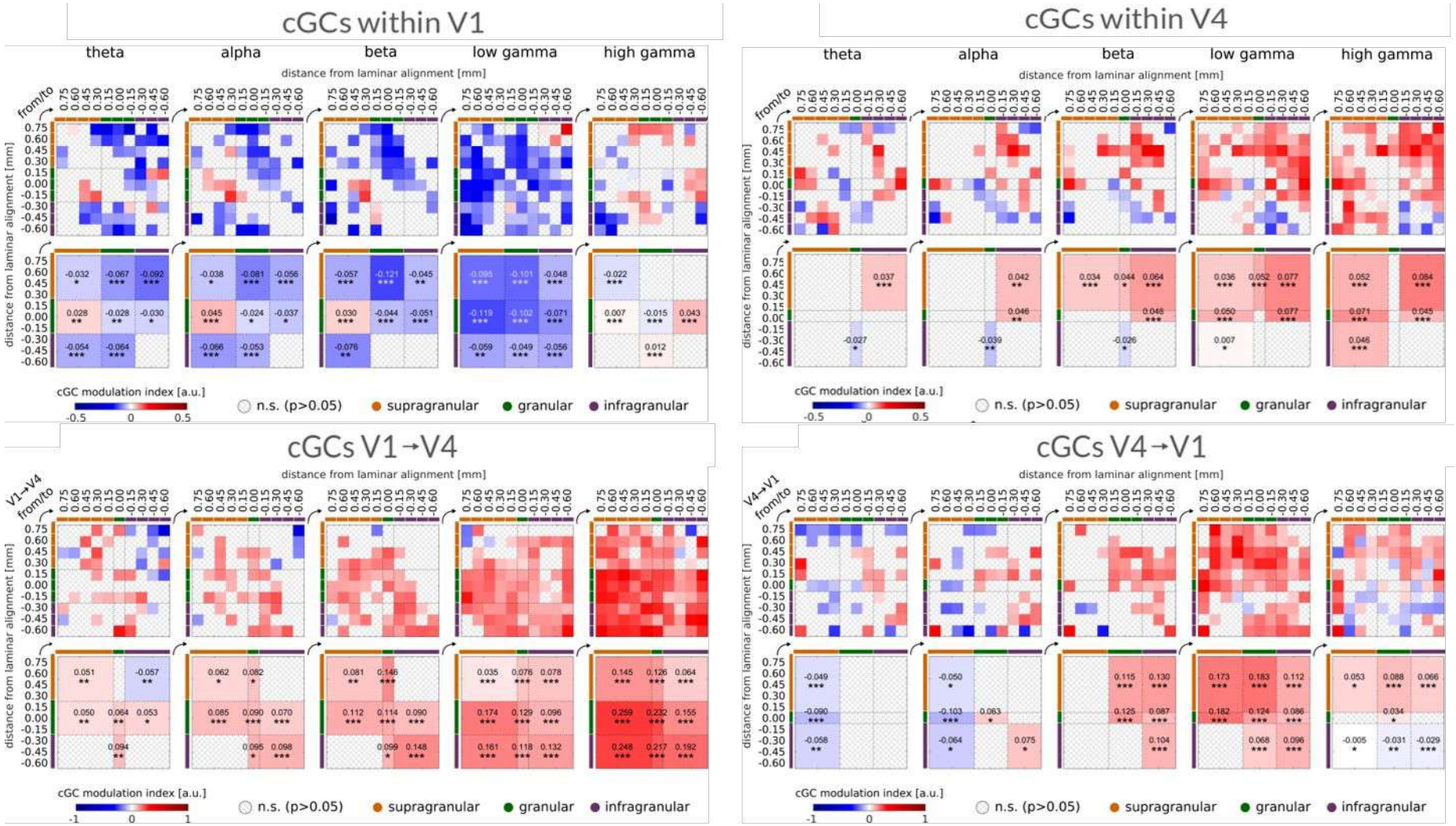








Visual Attention / Granger Causality

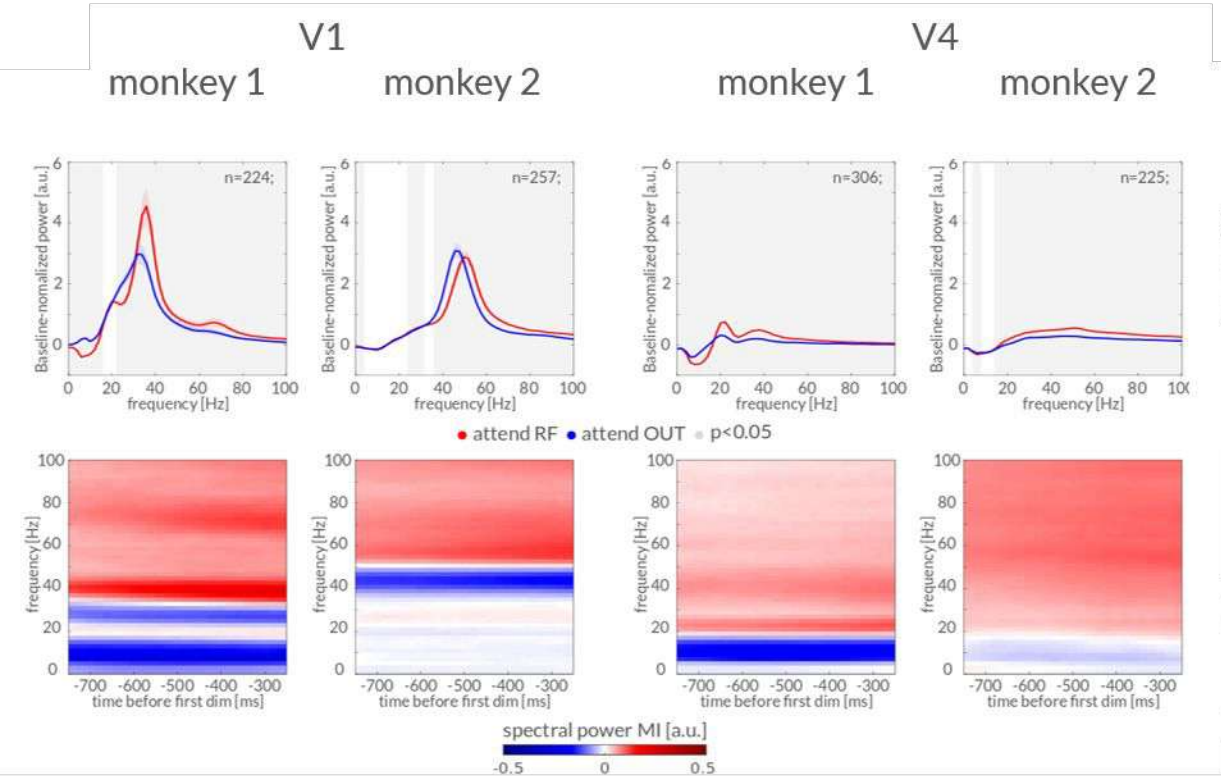


Outline

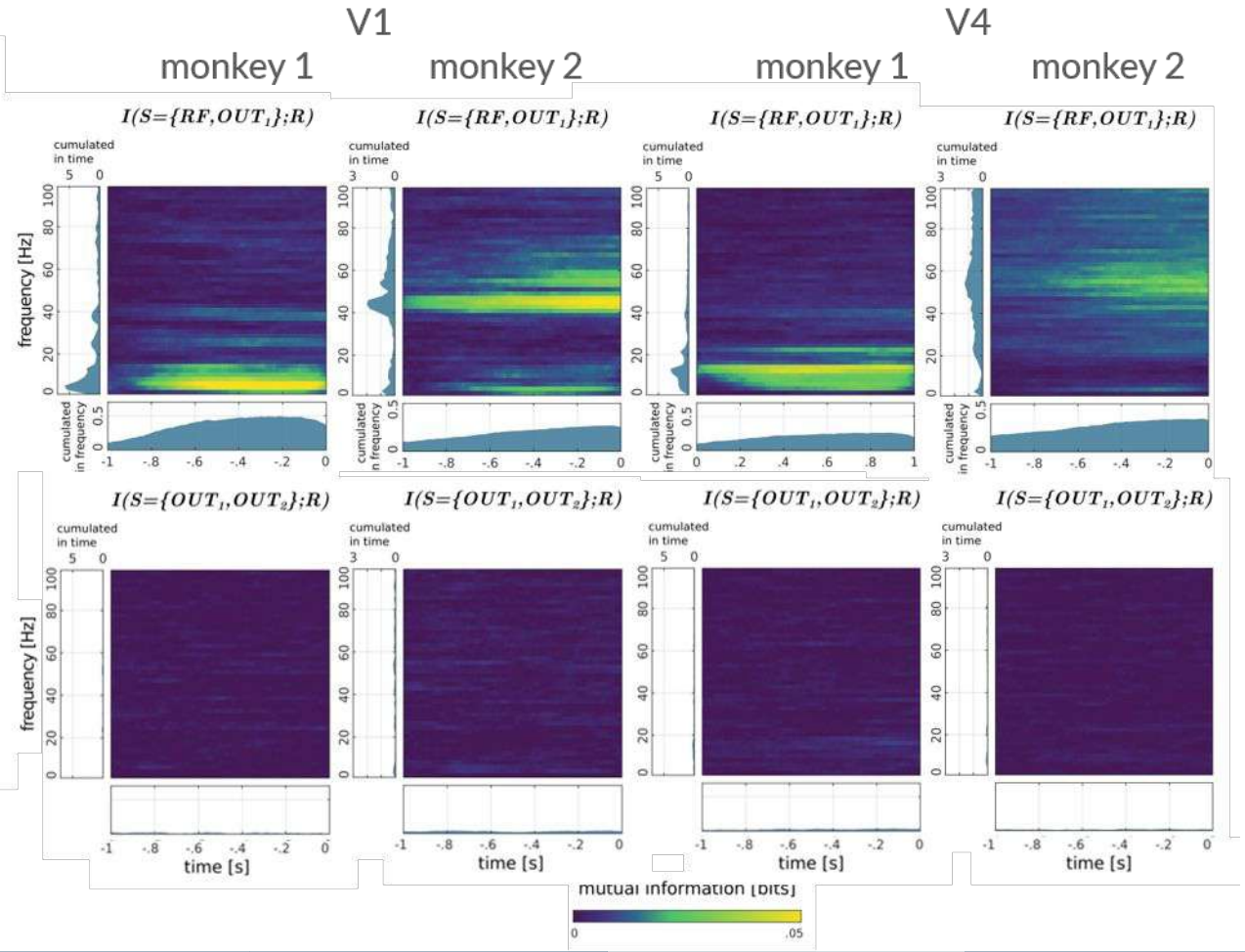
- ***Preliminary stages***
- ***Spectral power and attention***
- ***Spectral coherence and attention***
- ***Granger-causality and attention***
- ***Results summary***
- *Conclusions*

Visual Attention / Results summary (1)

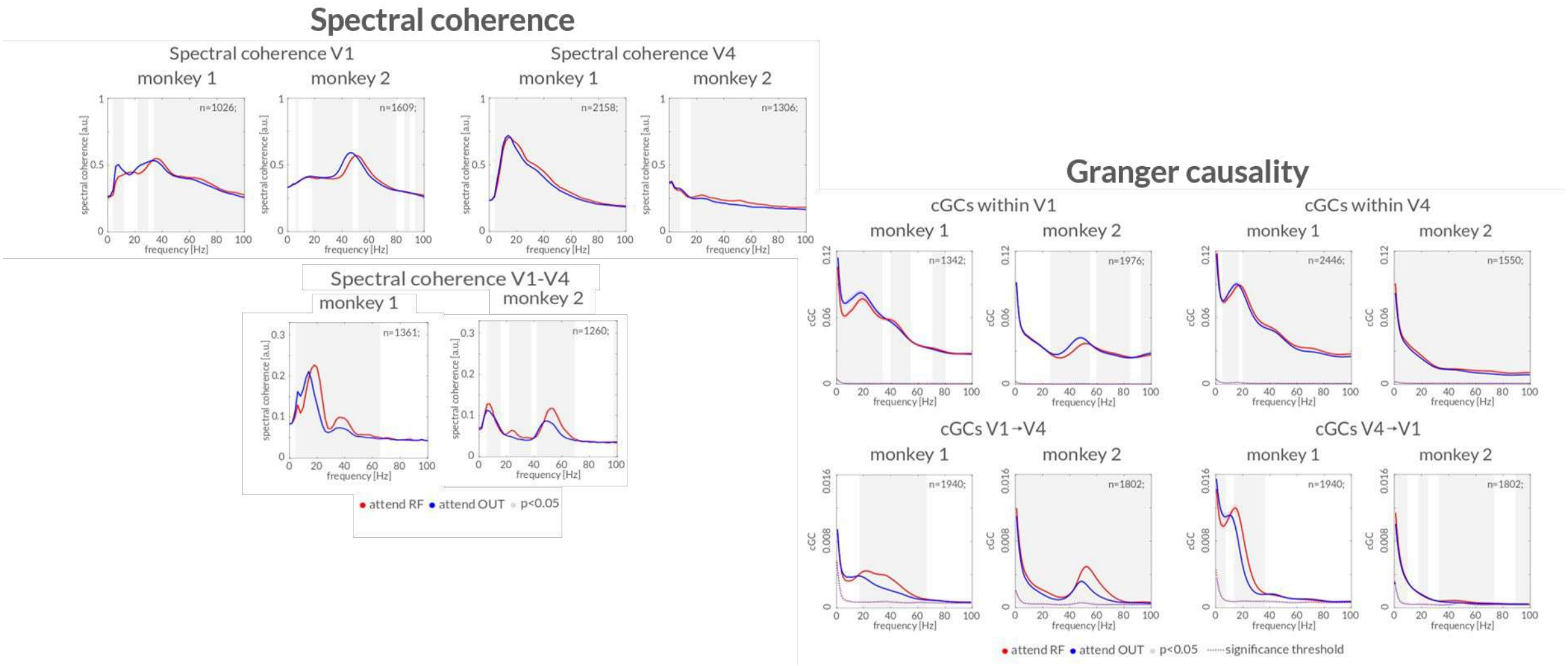
Spectral power



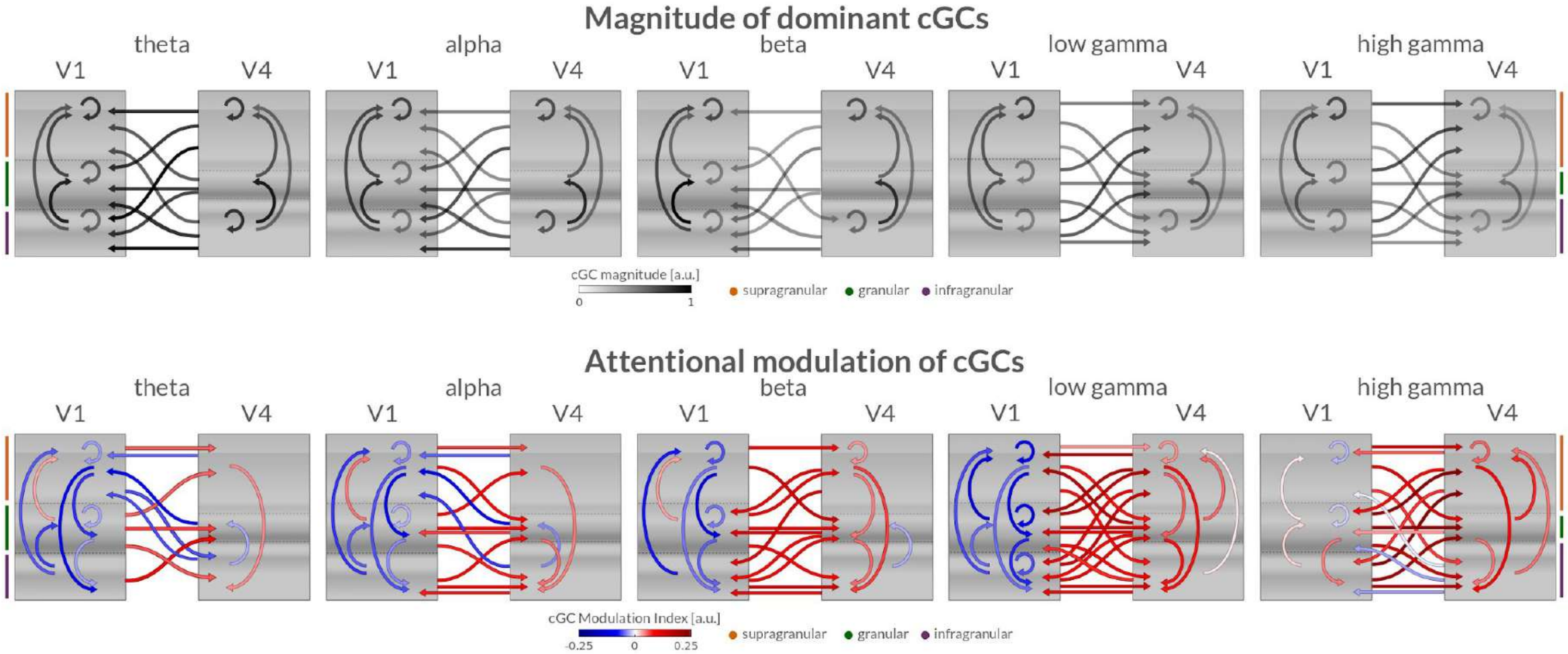
Mutual information



Visual Attention / Results summary (2)



Visual Attention / Results summary (3)



Visual Attention / Conclusions

Conclusions

- ***We applied spectral power/coherence analyses***
  - → *Attention mainly* ***increases*** *spectral power and coherence in* ***gamma-band****;*
  - → *Spectral modulation* ***is informative about attended stimuli****;*
- ***We computed GC directed influences across depths at different frequencies***
  - → *GCs* ***within V1****,* ***within V4****, showed more distinct* ***depth-specificity****;*
  - → *GCs* ***between V1-V4*** *showed most prominent* ***frequency-segregation****.*

Future directions

- *Additional* ***visual structures*** *such as V2 – thalamic nuclei (pulvinar);*
- *Different* ***visual features / tasks****;*
- *More detailed causality/****information-transfer analyses****.*

Thank you for your *attention*.

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Thank you for your *attention*.